VIE ET MILIEU - LIFE AND ENVIRONMENT, 2016, 66 (3-4): 325-331

CARBON FLOWS AND INTERACTION STRENGTH IN AQUATIC FOOD WEB MODELS

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FOOD WEB
CARBON FLOW
INTERACTION STRENGTH
TOPOLOGY
NETWORK ANALYSIS

ABSTRACT. – We studied 25 published marine food web models. We compared the sizes of carbon flows to the strength of interactions inferred by a topological measure. We determined which network properties correlate with a significant relationship between major flows and strong interactions. It is concluded that small and dense networks show significant interaction between flows and interaction strength but in large and sparse networks it can be misleading to use carbon flows as a proxy for finding important interactions.

INTRODUCTION

Mathematical models can be powerful tools to better assess marine biodiversity, to clarify the mechanisms generating and maintaining variability, and to propose management scenarios for sustainable fisheries and systems-based conservation (Ulanowicz 1996, Paraskevopoulou *et al*. 2015, Rodríguez-Zaragoza *et al*. 2016). Since various organisms co-evolve and coexist in nature, we cannot always understand their ecology and evolution separately. Community-level approaches offer the advantage of detecting non-local and higher-level phenomena, while they are limited by the lack of detailed information such as those in single-species approaches (genetics, demography, population biology).

Marine food webs provide a holistic view on the structure and the organization of marine ecosystems. Studying the whole system of trophic interactions may reveal higher-level patterns and phenomena that are not understandable if solely focusing on a single species or a single predator-prey interaction (Ulanowicz 1995). Some key issues are related to the pathways of energy across the system, how diverse are the potential routes (Mac Arthur 1955), what is the amount of cycling (Finn 1976), and how organized is it according to several particular macroscopic indices (*e.g*. Ulanowicz 1996). This kind of information can help to assess the maturity and vulnerability of marine systems and to quantify critically important system components.

One particular issue of great interest in current community ecology is to assess and model the strength of ecological interactions. Theoretical as well as empirical investigations provided a lot of knowledge here (*e.g*. about the importance of weak links) but there are still many open questions. For example, how are weak and strong links distributed in food webs.

Food webs can be modelled by directed and undirected (*i.e*. symmetric) trophic network models, whether we want to consider the flow direction of energy or we only want to see whether an interaction among two species exists. Taking direction into account provides a more realistic view, emphasizing carbon transfers, while the undirected network represents a mixture of various effects, in a more general way. Similarly, models can have weighted and unweighted (*i.e*. binary) interactions, whether we want to consider the amount of energy along a trophic flow or we only want to see whether it is present or not (Fig. 1). Weighting can be based on carbon flows, interaction strength values or even probabilities (see Jordán & Molnár 1999, Rushdi & Hassan 2016). There are pros and cons for both approaches, depending on model complexity, data availability and generality. For example, weighting can add a lot to realism if data are available. Yet, if the strengths of interactions change very frequently (like seasonally), a binary network model can be a more robust description of the system.

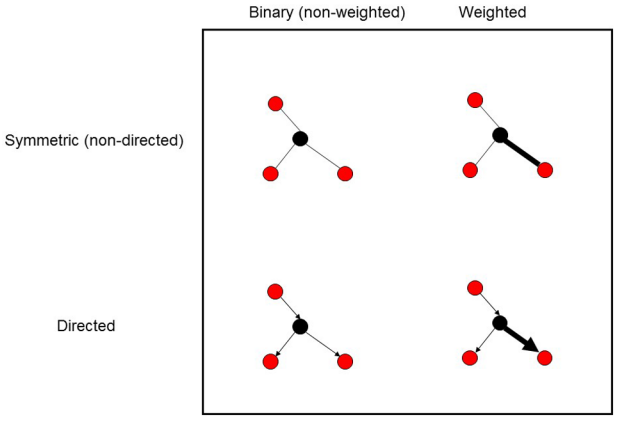

Fig. 1. – Diagram illustrating the four versions of networks we studied. For each of the four, we determined interaction strength based on a centrality approach.

Table I.– The list of the 25 food webs analysed in this study, their reference, whether their major flows are significantly central („signif", where S and NS stand for significant and non-significant, respectively) and some network properties (N = number of nodes, d = density, cc = clustering, avd = average distance).

WEB	Ref	Signif	N	d	cc	avd
Baltic	Baird *et al.* 1991	S	13	9.626	6.108	2.115
Benguela	Heymans and Baird 2000	NS	22	4.882	3.888	2.013
Bohai	Yi *et al*. 2005	S	12	0.124	0.611	1.409
Celestun	Vega-Cendejas and Arreguín-Sánchez 2001	S	19	11.099	11.096	1.544
Chesapeake (sum)	Baird and Ulanowicz 1989	S	33	676.918	1642.407	2.655
Crystal	Ulanowicz 1996	S	15	0.903	0.939	1.619
Cypress (dry)	Ulanowicz *et al*. 1997	NS	71	1.159	1.395	1.781
Ems	Baird *et al*. 1991	S	14	2.776	6.282	1.465
Everglades	Ulanowicz *et al*. 2000	S	69	8.458	18.586	1.636
Florida	Ulanowicz *et al*. 1998	NS	128	0.392	0.707	1.776
Kromme	Baird and Ulanowicz 1993	S	14	17.213	3.109	2.385
Kuosheng	Lin *et al.* 2004	NS	17	0.101	0.462	1.772
Mangrove (dry)	Ulanowicz *et al*. 1999	NS	97	1.004	1.477	1.693
Maspalomas	Almunia *et al.* 1999	S	24	24757.441	7873.385	1.819
Michigan	Krause and Mason, unpublished	NS	39	49.128	70.343	1.800
Mondego	Patrício *et al*. 2004	NS	46	10.188	4.811	1.662
Narragansett	Monaco and Ulanowicz 1997	S	35	5868.633	2443.541	1.657
Ontario	Christensen 1995	NS	13	15.256	23.768	1.859
Peruvian	Baird *et al*. 1991	S	15	72.423	135.942	2.162
Prince William	Okey and Wright 2004	NS	51	6.860	9.194	1.668
Rhode	Correll	S	20	1955.028	1364.440	1.830
StMarks	Baird *et al*. 1998	NS	54	1.416	2.863	1.761
Swartkops	Baird *et al.* 1991	S	14	20.512	2.409	2.484
Tongoy	Ortiz and Wolff 2002	NS	23	0.061	0.376	1.798
Ythan	Baird and Ulanowicz 1993	S	13	20.754	2.641	2.692

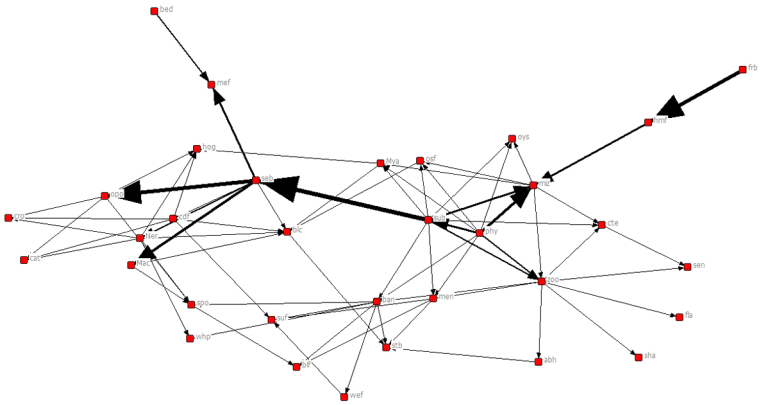

Fig. 2. – The Chesapeake Bay food web, illustrating directed and weighted links. The network is visualized by the spring embedding algorithm, not by the conventional way, based on trophic levels (*i.e*. producers at the bottom and top predators at the top). The abbreviations for the trophic groups are: phytoplankton (phy); suspended bacteria (sub); sediment bacteria (seb); benthic diatoms (bed); free bacteria (frb); heterotrophic microflagellates (hmf); microzooplankton (miz); zooplankton (zoo); ctenophore (cte); sea nettle (sen); other suspension feeders (osf); Mya (Mya); oysters (oys); other polychaetes (opo); Nereis (Ner); *Macoma* spp. (Mac); meiofauna (mef); crustacean deposit feeders (cdf); blue crab (blc); fish larvae (fla); alewife and blue herring (abh); bay anchovy (ban); menhaden (men); shad (sha); croaker (cro); hog choker (hog); spot (spo); white perch (whp); catfish (cat); bluefish (blf); weakfish (wef); summer flounder (suf); striped bass (stb).

Instead of favoring one particular kind of modelling approach, one needs to understand what is the relationship among different models (Vasas & Jordán 2006, Scotti *et al*. 2007). In this paper, we looked at a set of trophic networks in two different ways and compared the results. We analyzed 25 published marine trophic networks. First, we determined strong and weak interactions in the flow matrix of each network. Second, we determined critical interactions in the directed binary matrix of the same network models. Then, we determined whether the two correspond to each other. Finally, we studied what kinds of networks show statistically significant correspondence. For this, we used macroscopic topological network properties (see also Jordán *et al*. 2006).

DATA

We analyzed a set of 25 marine trophic networks published in the last decades. The references are given in Table I. All networks are weighted, providing information about carbon transfers between trophic components. The ecosystems studied here are marine, estuarine and freshwater systems. For example, Fig. 2 shows the directed and weighted carbon flow network of the Chesapeake Bay ecosystem (based on Baird & Ulanowicz 1989).

METHODS

The **C** matrix contains carbon flow values between system components. This is a sparse graph, with links only between pairs of predator and prey species.

In order to structurally assess the relative importance of links in the networks, we used the (weighted) topological importance measure (Jordán *et al*. 2003). The interaction effect from one species i on the other species j can be calculated as follows. First, we define a_{ij}^m as the effect of i on j when i can reach j in m steps. If i can reach j in one step, then a_{ij}^1 denotes the direct effect of i on j, which in turn equals $1/D_j$, where D_j is the number of interacting partners of j. We assume that indirect chain effects (i.e. a_{ij}^m with $m > 1$) are multiplicative and additive. For instance, we want to determine the effect of i on j in 2 steps, and there are two such 2-step pathways from i to j: one is through k and the other is through h. The effects of i on j through k is defined as the product of two direct effects a_{ik}^1 and a_{kj}^1. Likewise, the effect of i on j through h equals to the product of a_{ih}^1 and a_{hj}^1. To determine the 2-step effect of i on j (i.e. a_{ij}^2), we simply sum up those two individual 2-step effects (i.e. $a_{ik}^1 a_{kj}^{1+}+a_{ih}^1 a_{hk}^1$). The interaction effect of species i on species j up to n steps (E_{ij}^n) is the average of the 1-step effect, 2-step effect up to n-step effect:

$$E_{ij}^n = \frac{1}{n}\sum_{m=1}^{n} a_{ij}^m \quad (1)$$

Equation (1) is defined for unweighted networks where all links carry equal weights. For weighted networks, we need to modify how direct or one-step effects are defined:

$$a_{ij}^1 = \frac{w_{ij}}{\sum_h w_{hj}} \quad (2)$$

where w_{ij} is the weight of the link connecting species i and j; and h denotes for the interacting partner of species j. Thus, the denominator of equation (2) represents the sum of link weights connecting to species j. All else are the same as the unweighted version.

In this paper, we calculated the interaction effect between species pairs up to 3 steps for both the unweighted (TI^3) and the weighted version (WI^3) of the food web, by both considering ($dirTI^3$, $dirWI^3$) and neglecting (TI^3, WI^3) the direction of flows. Earlier studies suggest that indirect effects of two and three steps are generally of interest but longer pathways only rarely make a qualitative difference in results (see Jordán *et al*. 2003). These indices can be calculated by the Cosbi Graph software (Valentini & Jordán 2010).

The **D** matrix shows the interaction strength values for these four approaches. These are complete matrices, since indirect

Table II. – Kendall rank correlation coefficients between the normalized flow value and the normalized interaction effect under various scenarios: undirected and unweighted (TI^3), directed and unweighted ($dirTI^3$), undirected and weighted (WI^3), directed and weighted ($dirWI^3$). In the parentheses are the corresponding p-values. Bold numbers mean a significant fit of large flows to strong interactions.

Food web	TI^3	$dirTI^3$	WI^3	$dirWI^3$
Baltic	**0.181 (0.08)**	**0.099 (0.51)**	0.488 (< 0.01)	0.475 (< 0.01)
Benguela	**0.022 (0.67)**	0.248 (< 0.01)	0.449 (< 0.01)	0.658 (< 0.01)
Bohai	**0.016 (0.85)**	**0.096 (0.41)**	0.566 (< 0.01)	0.682 (< 0.01)
Celestun	**–0.012 (0.83)**	**–0.042 (0.59)**	0.387 (< 0.01)	0.428 (< 0.01)
Chesapeake	**–0.010 (0.88)**	**–0.128 (0.17)**	0.370 (< 0.01)	0.254 (< 0.01)
Crystal	**0.006 (0.93)**	**0.201 (0.06)**	0.467 (< 0.01)	0.628 (< 0.01)
Cypress	**–0.002 (0.90)**	–0.120 (< 0.01)	0.347 (< 0.01)	0.363 (< 0.01)
Ems	**–0.028 (0.79)**	**–0.318 (0.03)**	0.384 (< 0.01)	**0.143 (0.34)**
Everglades	**0.006 (0.73)**	**0.005 (0.81)**	0.452 (< 0.01)	0.387 (< 0.01)
Florida	0.051 (< 0.01)	–0.135 (< 0.01)	0.372 (< 0.01)	0.355 (< 0.01)
Kromme	**0.193 (0.06)**	**0.358 (0.02)**	0.450 (< 0.01)	0.604 (< 0.01)
Kuosheng	**0.016 (0.82)**	0.326 (< 0.01)	0.591 (< 0.01)	0.768 (< 0.01)
Mangrove	**0.017 (0.18)**	–0.101 (< 0.01)	0.288 (< 0.01)	0.298 (< 0.01)
Maspalomas	**–0.057 (0.30)**	**0.046 (0.55)**	0.403 (< 0.01)	0.481 (< 0.01)
Michigan	**–0.006 (0.85)**	–0.138 (< 0.01)	0.396 (< 0.01)	0.340 (< 0.01)
Mondego	**0.048 (0.05)**	–0.143 (< 0.01)	0.361 (< 0.01)	0.208 (< 0.01)
Narragansett	**0.037 (0.26)**	**0.051 (0.26)**	0.329 (< 0.01)	0.380 (< 0.01)
Ontario	**–0.039 (0.70)**	–0.396 (< 0.01)	0.250 (0.01)	0.499 (< 0.01)
Peruvian	**0.153 (0.07)**	**–0.202 (0.10)**	0.453 (< 0.01)	0.479 (< 0.01)
Prince William	**0.012 (0.60)**	–0.119 (< 0.01)	0.328 (< 0.01)	0.298 (< 0.01)
Rhode	**0.041 (0.57)**	**0.044 (0.65)**	0.503 (< 0.01)	0.527 (< 0.01)
StMarks	**0.007 (0.77)**	–0.133 (< 0.01)	0.370 (< 0.01)	0.289 (< 0.01)
Swartkops	**0.065 (0.56)**	**0.058 (0.72)**	0.479 (< 0.01)	0.544 (< 0.01)
Tongoy	**0.039 (0.48)**	0.261 (< 0.01)	0.598 (< 0.01)	0.780 (< 0.01)
Ythan	**0.121 (0.31)**	**–0.106 (0.54)**	0.561 (< 0.01)	0.493 (< 0.01)

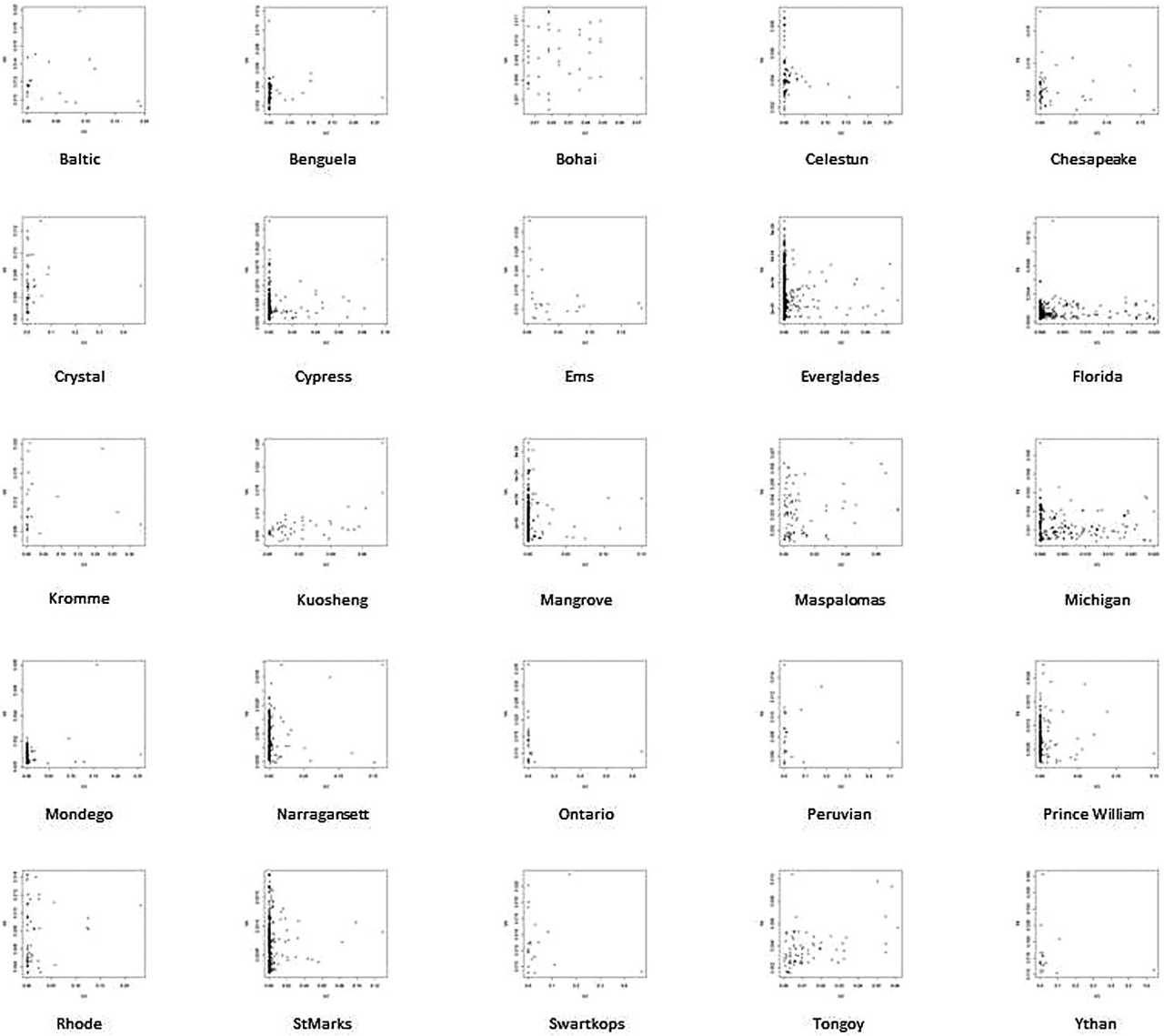

Fig. 3. – The plots of interaction strength values (measured here by dirTI[3]; on the y axis) against carbon flows (on the x axis) for the 25 food webs (see statistics in the second column of Table II).

interactions (considered up to three steps) make a connection between any two species. Strong interactions determined in this matrix can be called central interactions.

Both the **C** matrix and the four derived **D** matrices were normalized (individual values divided by the total sum) and the non-zero elements of **C** were compared to the corresponding elements in **D**. Thus, we were interested only in direct interactions among trophic compartments (an *ij* element that is zero in **C** but non-zero in **D** corresponds to an indirect effect). We did not consider the self-ties in the **D** matrix.

We performed Kendall rank correlation for assessing whether the ranks of interactions significantly differ in the **C** and **D** matrices (at $p = 0.05$). High correlation values (max = 1) show that strong flows are in topologically more central positions in the network, while low correlation values (min = –1) show that they are peripherial. When $p < 0.05$, we can say that the correlation is significant.

We analyzed four versions of the **D** matrix, the combinations of directed/undirected and weighted/unweighted links. In the case of weighted undirected links, their weight was defined as the sum of the two potential directed links (*ij* and *ji*).

Furthermore, we were interested in what types of networks (as measured by various network properties) show the significant relationship between the **C** and **D** matrices. We described our networks by macroscopic properties like the number of nodes (N), average distance (avd), clustering coefficient (cc) and density (d). We performed Wilcoxon rank sum test for statistical analysis. This determines whether the median values of significant and non-significant networks differ for these particular network properties.

RESULTS

The results of comparing the **C** and **D** matrices (size of flows to topological strength of interactions) are summarized in Table II and shown (only for the binary, directed case) in Fig. 3. In the undirected and weighted case (WI^3), all ranks were significantly similar: as WI is not independent of the flow magnitudes, this is not surprising, this method is just based on undirected flows. In the directed and weighted case ($dirWI^3$), there was one exception (Ems River). In the undirected and unweighted case (TI^3), only one network showed significant correlation (Florida Bay). The interesting case was the directed and unweighted approach ($dirTI^3$): here, the significance of the correlation was divided in two groups and this was the case where we needed to look for the relationship between network properties.

We see that small carbon flows can be in either central or peripherial network positions, while large carbon flows are always central. This reinforces dynamical simulations that highlight the potential importance of weak links (Scotti *et al*. 2012).

We have found that the networks that show significant correlation between link strength and centrality are different in the number of nodes (W = 30, p = 0.01077) and density (W = 121, p = 0.01521), marginally different in clustering (W = 110, p = 0.07487) and not different in average distance (W = 84, p = 0.7267). Fig. 4 summarizes these results. The significant correlations suggest that the size of the carbon flow between two nodes is a better predictor of their strong structural dependence in smaller networks that are composed by a larger number of links (higher density). We have, thus, detected a scale-dependence of this correlation.

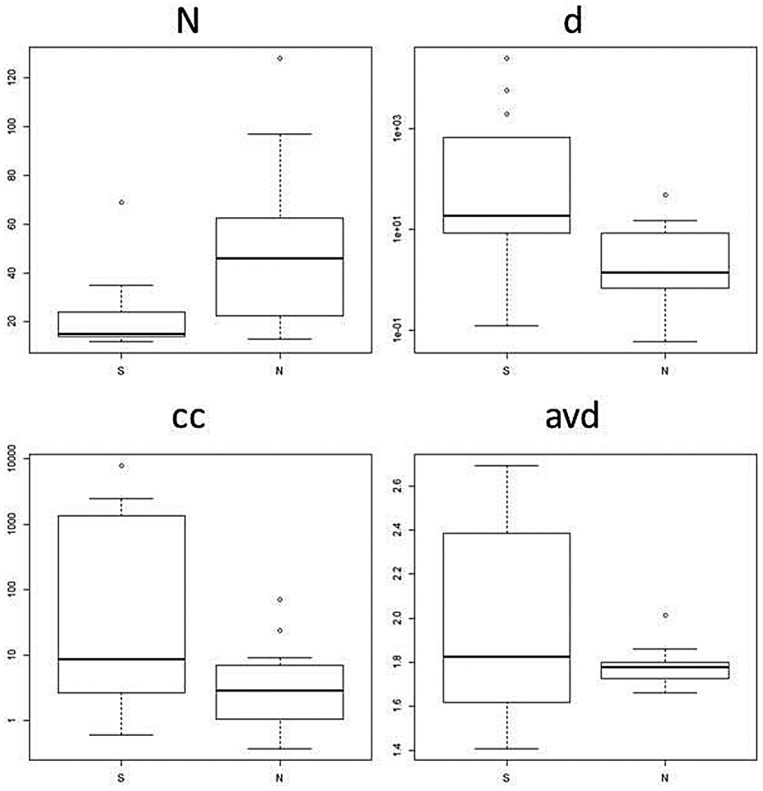

Fig. 4. – Relationships between the significance of the flow vs interaction strength correlation (S stands for significant and N stands for non-significant) and network properties (N = number of nodes, d = density, cc = clustering, avd = average distance).

CONCLUSIONS

There is a long-standing interest in the patterns of strong links in food webs. For example, there is a major interest in the relationship between energetics and stability in food webs (DeRuiter *et al*. 1996) and it was suggested that stronger links must be parts of longer loops in stable food webs (Neutel *et al*. 2002). The distribution of link strength values can be related also to trophic height (Scotti *et al*. 2009). In several cases, both short-term and long-term changes in ecosystems mean only the modification of relative interaction strength values of a topologically almost constant network (see D'Alelio *et al*. 2016).

In order to better understand the role of trophic interactions in shaping ecological communities, it is a question of interest to see how do major carbon flows coincide with topologically strongly related pairs of species. Network analysis is a helpful tool here, and studying the combination of different kinds of information (direction, weight) offers an insight here. There is a wide variety of network analytical techniques and it is a current issue how to understand their biological significance and how to choose the adequate method to a particular problem (Navia *et al*. 2016, McDonald-Madden *et al*. 2016). The index we used is one of the best performing indices in the literature (Pocock *et al*. 2011).

Carbon flows are considered as weighted and directed interactions among a pair of trophic compartments, so it is clear that weighted measures of interaction strength (WI^3, $dirWI^3$) correlate almost always with the flow pattern. It is also clearly shown that the undirected and unweighted (TI^3) approach to interaction strength correlates little with the flow pattern. The interesting case is when direction is still considered but the strength of the links is not (directed, unweighted, $dirTI^3$). In this case, we have found that major flows fit to the most important interactions mostly in smaller (lower N) and denser (higher d) networks. This implies that in a large and spare network the carbon flow

analysis is a poorer predictor of key interactions in the system.

ACKNOWLEDGMENTS. – FJ was supported by the National Research, Development and Innovation Office – NKFIH, grant number K 116071. We are grateful for the excellent comments of two anonymous Referees.

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Received on March 20, 2016
Accepted on August 20, 2016
Associate editor: N Coineau